Neural and Computational Mechanisms of Perceptual Decisions Between Multiple Alternatives Based on Multiple Sources of Evidence

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Summary

The goal of the project was to elucidate computational mechanisms underlying perceptual decisions between multiple alternatives as well as their neural implementation. To this end we have performed behavioral experiments in humans as well as combined behavioral and neurophysiological experiments in non-human primates. Computational modeling techniques were used for addressing the computational mechanisms underlying the perceptual decisions. A multi-alternative version of the random dot motion direction discrimination task, using a multi-component stimulus, was found to provide a rich behavioral dataset, spanning accuracy levels from chance to perfect and a wide range of mean response times while providing simultaneous experimental control over how much sensory evidence is provided for each of the alternatives. The behavior was found to be consistent with a number of integration-to-threshold mechanisms, including integration with and without leakage, feedforward as well as feedback inhibition mechanisms for mediating the competition between the alternatives, and linear as well as nonlinear mechanisms for combining the signals associated with the different alternatives. While these different mechanisms produce virtually indistinguishable decision behavior, we have been able to demonstrate that the internal dynamics of these mechanisms are quite different, which should be addressable by performing high-resolution recordings of brain activity while decisions are being made. To this end we have trained non-human primates to perform the same decision task and we have performed multi-electrode recordings of decision-related activity in parietal cortex. Data collection and analysis are currently being finalized to be able to apply them to discriminating between different decision models. We have also addressed how different decision mechanisms relate to multi-alternative decision theory.

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Report

Human behavior
A multi-alternative version of the random dot motion direction discrimination task, using a multi-component stimulus, was used to address the computational and neural mechanisms underlying perceptual decisions between multiple alternatives. Briefly, subjects were asked to watch a visual noise stimulus with three embedded components of coherent motion and to indicate the direction of the strongest component. The three motion coherences were randomly chosen from trial to trial and the subjects' choices and response times were measured (see Niwa & Ditterich, 2008 for further details). The resulting behavior spanned the full range of accuracy levels (from chance to perfect), a wide range of mean response times (from approx. 600 ms to approx. 1,600 ms), and the simultaneous manipulation of how much sensory evidence was provided for each of the alternatives allowed an independent manipulation of either accuracy or response time.

Computational models accounting for the human behavior
The behavior was found to be consistent with an integration-to-threshold model with three integrators (one for each choice option), which all accumulate a different linear combination of three task-relevant sensory evidence signals. As soon as one of the integrators reaches a critical decision threshold the choice is determined and the decision process terminates (see Niwa & Ditterich, 2008 for further details).

In the meanwhile we have been able to demonstrate that this is only one of a number of possible integration-to-threshold mechanisms that could be responsible for the observed behavior. The different alternatives include integrators with and without leakage, feedforward as well as feedback inhibition mechanisms for mediating the competition between the integrators, as well as linear and nonlinear ways of combining the integrator signals. The feedforward inhibition model published in Niwa & Ditterich (2008) and the feedback inhibition-based Leaky, Competing Accumulator (LCA) model (Usher & McClelland, 2001) are both examples of decision mechanisms relying on linear signal combinations, whereas the implementations of MSPRT that have been proposed by Bogacz & Gurney (2007) and by Bogacz (2009) make use of nonlinear signal combinations. While these different mechanisms are virtually indistinguishable in terms of the produced decision behavior, their internal dynamics can be shown to be quite different. They make different predictions how the states of the integrators should evolve over time and also for the correlation structure of the input signals to the integrators. It should therefore be possible to discriminate between these mechanisms based on simultaneous high-resolution (both spatial and temporal) recordings of decision-related brain activity associated with different alternatives. It is further possible to address how the different decision mechanisms are related to multi-alternative decision theory. For example, for the simpler case of decisions between two alternatives it can be shown that the decision should be made on the basis of the likelihood ratio between the two alternatives and that, if the decision is based on sequential sampling of independent sensory evidence, the decision process should be terminated when the likelihood ratio exceeds a particular threshold. This algorithm, the sequential probability ratio test (SPRT), has been proven to guarantee the lowest possible average sample size (or mean decision time) for any desired accuracy level (Wald, 1945). Furthermore, the drift

diffusion model, a popular mathematical psychology model of decisions between two alternatives, is an implementation of this algorithm if the drift rate is proportional to the logarithm of the likelihood ratio, and the difference between the activities of two pools of opposing sensory neurons has been shown to approximate this property (Gold & Shadlen, 2001). The situation is more complicated when more than two alternatives are available. In this case, the optimal algorithm for any desired accuracy level is still unknown. It has been shown that an extension of SPRT, the multi-hypothesis sequential probability ratio test (MSPRT) is asymptotically optimal in the case of a negligible error rate (Dragalin et al., 1999). However, human decision makers are rarely perfect. I have extended this framework to discuss what kind of statistical tests are implemented or approximated by different decision mechanisms and how their optimality compares in a biologically relevant range of error rates. A manuscript is currently being finalized and will be provided when published.

Neural recordings from non-human primates
To be able to perform high-resolution recordings of decision-related brain activity, three non-human primates were trained to perform the same task as our human observers. Although they did not quite reach the same accuracy level (approx. 80% in humans and approx. 70% in monkeys) and although they were overall faster than the human observers (mean response times ranging from approx. 600 ms to approx. 1,000 ms), the overall behavioral pattern was qualitatively similar. Multi-electrode recordings were performed in the lateral intraparietal area (LIP) in parietal association cortex. Neurons in this area were previously shown to carry decision-related activity in a motion discrimination task (Roitman & Shadlen, 2002). Whenever possible, simultaneous recordings from at least two neurons, associated with either the same or with different choice options, were performed. In addition to action potentials, local field potentials (LFPs) were also recorded. The basic firing rate pattern of the recorded neurons turned out to be consistent with previous observations: approx. 200 ms after motion onset, the firing rate shows a coherence-dependent ramping behavior (see Fig. 1 for preliminary data) and, when the neuron is associated with the chosen option, reaches a stereotyped level immediately prior to the monkey's behavioral response (see Fig. 2).
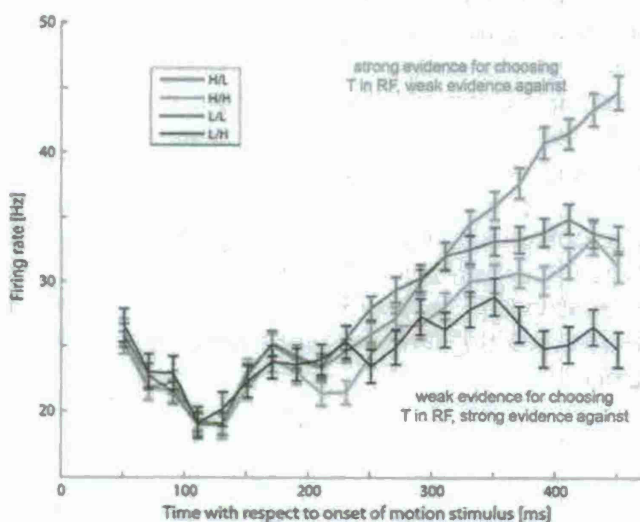

Fig. 1: Firing rate in LIP shows ramping activity approx. 200 ms after motion onset with the slope depending on motion coherences
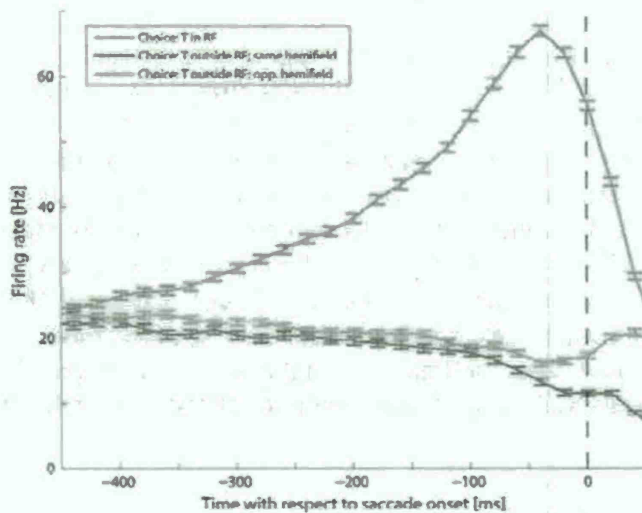
Fig. 2: Firing rate immediately prior to saccade onset (behavioral response for reporting the choice) is choice-selective

Since we have used a 3-component stimulus, the slope of the initial ramp (between 250 and 400 ms after motion onset), which is assumed to reflect the accumulation of sensory evidence, is expected to be a function of the three relevant coherence levels. The difference between the coherence of the component providing evidence for picking a choice target inside the recorded neuron's response field and the average of the other two coherences turned out to be a major determining factor (see Fig. 3). This is what the model published in Niwa & Ditterich (2008) would predict. However, there are two other interesting features: The slopes have a clear positive offset (they are not zero for zero net coherence) and they can be quite different for the same net coherence (see the three symbols stacked on top of each other at zero net coherence). The first effect is not predicted by a feedforward inhibition model with perfect integrators and Churchland et al. (2008), who have also reported this phenomenon, have interpreted it as evidence for a top-down soft deadline signal. However, as discussed in Ditterich (2006), such a signal would be expected to have a strong impact on the shape of the response time (RT) distributions. Our preliminary data, however, do not provide any strong evidence for a major shortening of the tail of the RT distributions. Instead, preliminary modeling indicates that this offset could just be the consequence of the nonlinear properties of a biological integrator: it cannot represent negative values. The second observation (quite different slopes for the same net coherence) is also interesting because it could be an indication of a normalization process operating at the level of the decision circuitry. We are currently looking into this in more detail. The three symbols stacked on top of each other at zero net coherence belong, from top to bottom, to stimuli with no coherent motion, with coherent motion of 10% in each direction, and with coherent motion of 20% in each direction. Thus, the slope is actually decreasing with increasing coherence. The slope change therefore also cannot be explained by a feedback inhibition model, which would predict an effect in the opposite direction (higher coherence should be providing a stronger excitatory drive to the integrator).

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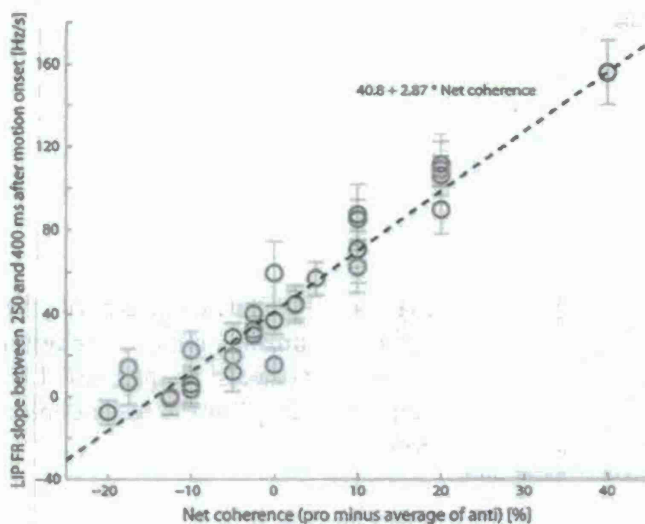
Fig. 3: Firing rate slopes as a function of net coherence. The color of the symbols indicates the sum of all three coherences (blue = low, red = high).

As mentioned above, different decision mechanisms make different predictions for the correlation structure of the input signals to the integrators. Our hope was that this correlation structure would show up in the correlation structure of the spike pattern emitted by two simultaneously recorded neurons that are coding for two different options. Unfortunately, the majority of pairs of neurons that code for two different options, which we have recorded so far, did not show any significant correlation in their spike timing. This can be interpreted a number of ways and only more detailed modeling can help us come up with an answer. Possible options include decision mechanisms that actually predict almost no correlation between the input signals to the integrators, or, since we are only recording two individual neurons out of probably quite large pools, the connections could be so sparse that correlations that should be there at the population level cannot be seen at the single neuron level. We have also recorded from pairs of neurons that code for the same option. The majority of these show the expected positive cross-correlation near zero lag (due to common, probably excitatory, input), but they also tend to show an unexpected, asymmetric negative cross-correlation at a relatively large lag of approx. 10 ms (see Fig. 4 for a typical example). This could indicate unexpected, directed inhibitory connections between neurons belonging to a particular decision pool, and we are currently looking into this finding in more detail.
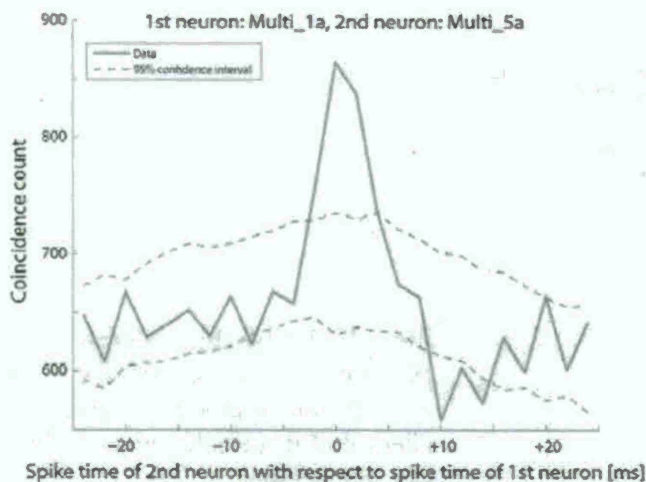
Fig. 4: Typical example of the spike time cross-correlation structure between a pair of LIP neurons coding for the same choice option

In addition to spiking activity we have also recorded local field potentials (LFPs). There is still considerable debate what exactly LFPs are, but there is some consensus that they are strongly influenced by dendritic activity and therefore might be considered a measure of the input to a brain area in contrast to the spiking activity, which reflects the output of the recorded neuron. We are still in the process of analyzing the LFPs, but preliminary results indicate that they contain information about the motion stimulus, that they do so before the spiking activity shows selectivity for the motion stimulus, and that what they are coding does not seem to be redundant with the information in the spiking activity. Fig. 5 shows the difference in the low-frequency power spectrum between trials with only low coherences and trials with only high coherences. (This is where we see the strongest effect in the LFPs in contrast to the firing rate, where the strongest effect is seen between trials with strong support/weak evidence against and weak support/strong evidence against.) The main effect is a reduction in the LFP power around 8 Hz for overall high coherence trials in the first 200 ms after motion onset. We are currently performing a more detailed quantitative analysis of this phenomenon.
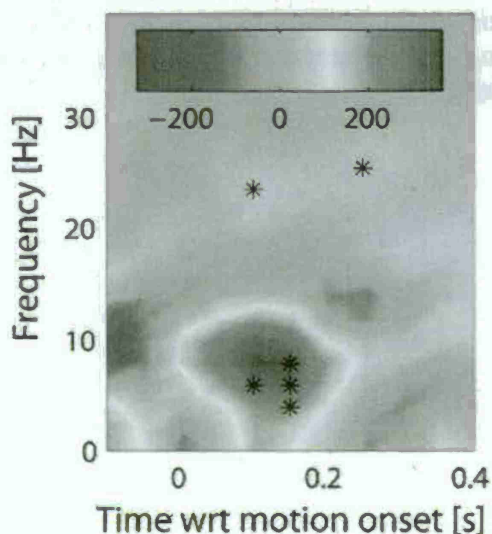
Fig. 5: Difference in LFP power between trials with only low coherences and trials with only high coherences. Stars indicate time/frequency combinations where the 95% confidence intervals of both spectra do not overlap.

We are currently in the process of finishing up the neural recordings and their analysis. We still need to combine the neural data and the modeling. Some preliminary results have been presented at last year's Society for Neuroscience Annual Meeting (Bollimunta & Ditterich, 2009). More results will be presented this year and publications will be provided as they become available.

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14. ABSTRACT
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